A NEW *IPOMOPSIS* (PALE MONIACEAE) FROM THE SOUTHWEST USA AND ADJACENT MEXICO

DIETER WILKEN Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105

Abstract

Ipomopsis longiflora subsp. **neomexicana**, a new subspecies, is distinguished from subsp. *longiflora* (Torr.) V. E. Grant and subsp. *australis* R. A. Fletcher and W. L. Wagner by its annual habit, ovaries with a modal number of 30 ovules, minutely winged seeds, and ellipsoid capsules that are about twice the length of the calyces. Subspecies *neomexicana* occurs in parts of the Great Basin and Chihuahuan Desert, ranging from southeastern Utah and southern Colorado through eastern Arizona and New Mexico into northern Mexico. The 3 subspecies are self-compatible, strongly self-pollinating, but have flowers that attract hawkmoths.

Ipomopsis longiflora (Torr.) V. E. Grant is based on a specimen (Holotype: NY!) collected by Edwin James "on the Canadian River," probably what is now the North Canadian River in Oklahoma (McKelvey 1956). Descriptions of Ipomopsis longiflora were given by Wilken (1986), Welsh et al. (1987), and Cronquist et al. (1984), the latter two under the name Gilia longiflora (Torr.) G. Don. The species is distinguished from all members of *Ipom*opsis by its sparsely glandular-puberulent herbage, pinnatifid leaves with 5-7 linear to narrowly oblong segments, open, paniculate inflorescences, glandular-puberulent calyx tubes, and white to pale blue salverform corollas that are 25-45 mm long. Ipomopsis longiflora is confused sometimes with the related I. laxiflora (J. M. Coult.) V. E. Grant, which has a smaller stature and corolla tubes between 8 and 20 mm long (Wilken 1986). Subspecies longiflora is a biennial of the western Great Plains, distributed from South Dakota to central Texas (Wilken 1986). It is characterized by narrowly ellipsoid capsules that are about the length of the calyx.

Fletcher and Wagner (1984) applied the name I. longiflora subsp. australis to plants with ovoid to broadly ellipsoid capsules that are equal to or that only slightly exceed the calyx. Fletcher and Wagner also reported differences in seed shape and calyx lobe vestiture. Subspecies australis occurs from "Mohave Co., Arizona, south and west of the Mogollon Plateau, to southwestern New Mexico as far east as Deming in Luna Co., New Mexico, and to northern Sonora" (Fletcher and Wagner 1984). However, Fletcher and Wagner did not study specimens of the species east of the Rocky Mountains. While reviewing specimens and conducting field work for the Flora of the Great Plains and Flora of North America projects, I noticed differences between plants of the Great Plains and those treated as subsp. longiflora by Fletcher and Wagner. Plants from the Great Plains are all assignable to the typical subspecies, but plants referred to subsp. *longiflora* by Fletcher and Wagner are recognized here as a new, morphologically and geographically distinct subspecies.

Ipomopsis longiflora (Torr.) V. E. Grant subsp. **neomexicana** Wilken, subsp. nov. (Fig. 1)— TYPE: USA, New Mexico: Sierra Co., Mitchell Point Road, 1.6 mi N of junction with Interstate 25, 14 mi N of Truth or Consequences. 15 May 1985, *Wilken 14323* (Holotype UNM; isotypes ARIZ, CAS, CS, RM, RSA, UC).

Herba annua foliosa, 20–52 cm alta. Folia caulina pinnatifida, 12–35 cm longa, supra glabri infra secus costas sparsim pubescentes; partes 5–7, anguste lineares, laterales distantes 5–19 mm longae, terminales 9–29 mm longa. Inflorescentia laxa subcorymbosa vel aliquantum rotundata; bracteae simplices vel subulatae, 7–15 mm longae. Calyces in statu florendi 6–9 mm longae, extus minute glandulosus, interne prope apices loborum puberulus. Corollae hypocrateriformes, 30–47 mm longae; lobis late obovatis vel rotundati, persaepe caesii, 7– 10 mm longi. Capsulae ellipsoidae, 10–15 mm longae, calyce 1.5–2plo longiorae. Semina anguste ellipsoidea, pallide flavo-brunea, 2.5–3 mm longa, ad apices minute alati.

Annual herb 20–52 cm tall, with one to four erect to ascending branches arising from below middle of central axis. Stems glabrous to sparsely invested with short, uniseriate, eglandular and glandular trichomes. Leaves 12–35 mm long, pinnatifid, with (3)5–7(9) linear segments ca. 1–2 mm wide, lateral segments 5–19 mm long, distal segments 9– 29 mm long, petioles 4–13 mm long; basal leaves in a rosette, senescent at anthesis; cauline leaves 18–35 mm long, gradually reduced upwards, subglabrous above, sometimes with minute trichomes bearing a terminal, globose cell, sparsely pubescent on lower surface of rachis and lateral segments, trichomes uniseriate and mostly eglandular. Inflores2001]

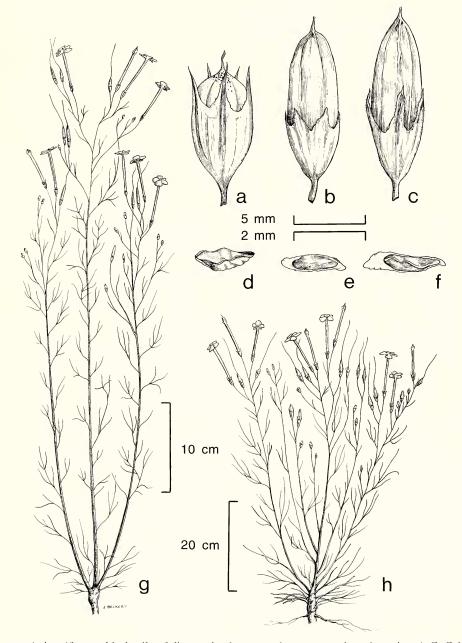


FIG. 1. *Ipomopsis longiflora*, with details of diagnostic characters that separate the subspecies. A-C. Calyx and fruit. A. ssp. *australis*. B. ssp. *neomexicana* C. ssp. *longiflora*. D-E Seeds. D. ssp. *australis*. E. ssp. *neomexicana* F. ssp. *longiflora*. G. Generalized habit of ssp. *longiflora*. H. Generalized habit of ssp. *neomexicana*.

cences indeterminate, paniculate, corymbiform to somewhat rounded, with flowers in loose, terminal clusters of 2–3; bracts simple, linear to aculeate, 7– 15 mm long; pedicels slender, 9–24 (30) mm long, sparsely glandular-puberulent, trichomes uniseriate with a terminal globose cell. *Calyces* 6–9 mm long, tube 3–6 mm long, lobes 2.5–4 mm long, narrowly acuminate, tube sparsely to moderately glandularpuberulent externally, lobe apices eglandular puberulent within, trichomes uniseriate and straight or slightly curled. *Corollas* salverform, 30–47 mm long, glabrous, tube white, lobes elliptic to subrotund, 7–10 mm long, usually pale bluish or bluish lavender, sometimes white, apices rounded to apiculate. *Ovary* 5–6 mm long, style 25–44 mm long, stigmas included in the tube, sometimes slightly exserted, stigmatic branches 2–3 mm long; ovules 8– 10 per locule. *Stamens* inserted unequally above mid-tube, 3–4 included, 1–2 slightly exserted, lower filaments subsessile to 4 mm long, upper filaments 1–3 mm long, anthers 2–3 mm long. *Pollen* white, sometimes bluish, grains subspheroidal, zonocolporate, colpi 6–8, exine striate or striate-reticulate near colpi. *Capsules* 10–15 mm long, 1.5–2 times longer than the fruiting calyx; seeds 2.5–3 mm long, yellowish brown, narrowly ellipsoid, dorsal margins and apices minutely winged.

Paratypes. USA, Arizona: Apache Co., 10 mi N of Springerville, Pase 1508 31 Aug 1965 (ASU), Coconino Co., Flagstaff, Hanson 128 11 Jun 1922 (LL, NY, TX), Mohave Co., Mociac Ranch, Cottam 4171 6 Jun 1929 (NY), Navajo Co., 5 mi N of Snowflake, Deaver 6490 12 Jul 1963 (ARIZ, ASU), Yavapai Co., Cornville, Jones 266 19 Sep 1922 (ARIZ); Colorado: Alamosa Co., 25 mi NE of Alamosa, Iltis 4352 11 Jul 1953 (RSA, WI), Costilla Co., N of Alamosa, Bethel, Willey & Clokey 4250 27 Jun 1921 (NY, POM, RM, US, WS), La Plata Co., Animas River, 2 mi S of Bondad, Ownbey 1445 17 Aug 1937 (NY, RM, UTC, WS), Montezuma Co., McElmo Canyon, Weber 7948 1 Sep 1952 (COLO, WS), Montrose Co., La Sal Creek, Gierisch 1381 21 Jun 1942 (RM), Saguache Co., Crestone, Ramaley 12089 18 Jul 1928 (RM); New Mexico, Bernalillo Co., Rio Puerco, Ripley & Barneby 2379 7 Oct 1939 (NY), Catron Co., E of Reserve, Clark s.n. 17 Aug 1942 (UNM), Doña Ana Co., 3 mi E of Las Cruces, Ward 66 9 Apr 1981 (LL, NMC, NY, TX), Eddy Co., 22 mi SW of Carlsbad, Waterfall 3750 14 Aug 1942 (NY), Grant Co., 8 mi W of Silver City, Barkley 14694 24 Sep 1944 (OKL), Guadalupe Co., 1 mi E of Santa Rosa, Clark 10016 18 Jun 1951 (UNM), Lincoln Co., 4 mi NW of Capitan, Stephens 25897 29 Jul 1968 (KANU), Luna Co., 5 mi S of Deming, Sands s.n. 6 Jun 1962 (UNM), McKinley Co., 7 mi NE of Borrego Pass, Marley 1575 21 Jun 1978 (UNM), Otero Co., 11 mi W of Cloudcroft, Waterfall 12951 22 Aug 1956 (ARIZ, US), Rio Arriba Co., near Española, Correll 50851 26 Jul 1979 (NY), San Juan Co., 4 mi N of La Plata, Spellenberg & Ward 6155 11 Aug 1981 (NMC), Sandoval Co., 12 mi N of San Ysido, Shultz & Shultz 1304 (NY, UTC), Santa Fe Co., 13 mi W of Pojoaque, Gentry 23037 6 Sep 1972 (ASU), Socorro Co., 5 mi W of Bingham, Dunn 5201 6 Oct 1948 (UNM), Taos Co., Ojo Caliente, Smith s.n. 30 Jul 1894 (WS), Torrance Co., 8 mi S of Estancia, Martin 4374 12 Sep 1960 (UNM), Valencia Co., El Morro Nat. Mon., Kayes 42 9 Jul 1978 (UNM); Texas, Brewster Co.: 2 mi E of Lajitas, Higgins 2763 25 May 1970 (NY), Culberson Co., near Van Horn, Warnock 388 20 Apr 1938 (TX), El Paso Co., Hueco Tanks, Powell & Powell 3005 12 Jul 1976 (TX), Hudspeth Co., 8 mi W of Sierra Blanca, Hitchcock 6775 25 Jun 1940 (NY, POM, UTC, WS), Presidio Co., 11 mi S of Marfa, Correll & Rollins 23651 19 Apr 1961 (NY TX); Utah, Garfield Co., 11.4 mi E of Escalante, Holmgren & Holmgren 4719 10 Aug 1970 (KANU, NY, US, UTC), Grand Co., Dead Horse Point, CarTABLE 1. COLLECTION DATA FOR CHROMOSOME COUNTS AND PHENOLOGY STUDIES OF *IPOMOPSIS LONGIFLORA*. Voucher specimens for chromosome counts are deposited at CS unless otherwise noted.

Subsp. *longiflora*. Colorado, Logan Co., US Highway 6, 2.8 mi E of junction with Interstate 76, 29 Sep 1982, *Wilken 13887*, 2n = 14; Nebraska, Sheridan Co., 0.8 mi N of Niobrara River, 12 Aug 1983. *Wilken 13988*, 2n = 14.

Subsp. *neomexicana*. Arizona, Apache Co., Hwy 666, 2 mi N of Zuni Wash, 21 May 1985, *Wilken 14422*, 2n =14, Coconino Co., between Wupatki Ruin and Sunset Crater, 8 Aug 1987, *Wilken 14844*, 2n = 14; Colorado, Alamosa Co., 5 mi E of Alamosa, 7 Jul 1986, *O'Kane 2464*; New Mexico, Sierra Co., Mitchell Point Rd, 1.6 mi N of junction with Interstate 25, 15 May 1985, *Wilken 14323*, 2n = 14; Texas, El Paso Co., El Paso, 28 Mar 1983, *Worthington 9651 2n* = 14, (UTEP).

Subsp. *australis*. Arizona, Gila Co., Hwy 60, N side of Gila River Bridge, 21 May 1985, *Wilken 14416*, 2n = 14, Hwy 77, 12 mi N of Globe, 20 May 1985, *Wilken 14414*, 2n = 14.

ter 1561 27 May 1940 (UTC), San Juan Co., near La Sal, *Flowers 2084* 7 Jun 1939 (NY). MEXICO, Chihuahua, 4.8 mi S of Samalayuca, *Hendrickson* 5783 19 Aug 1971 (TX), Coahuila, 10 mi s of Laguna del Rey, *Hendrickson 14158* 20 Sep 1974 (TX).

METHODS

677 specimens from 21 herbaria were studied (ARIZ, ASU, BRY, COLO, CS, KANU, KSU, LL, NEB, NMC, NY, OKL, POM, RM, RSA, TX, UNM, US, UTC, WI, WS). Eight quantitative characters were chosen for detailed study (Table 2). Measurements were made on a subset of specimens that represented the geographic range of each taxon. Sample sizes for each character varied, depending on the condition of specimens. Field studies were conducted in one to three populations of each subspecies (Table 1) to study population structure and to obtain seeds for assessing life history characteristics under controlled conditions, the breeding system, and chromosome number. Seeds were germinated in a greenhouse at Colorado State University, Fort Collins, Colorado in late November and transplanted to 6-inch diameter pots in early January. Plants of subsp. australis and subsp. neomexicana, which began bolting in March, completed their life cycles (April-May) under greenhouse conditions. Plants of subsp. longiflora continued to produce basal leaves throughout the spring and early summer months, but did not flower. Ten plants from each of two populations were retained under greenhouse conditions; a total of 21 additional plants were transplanted to a garden in July. Selfcompatibility and autogamous seed production relative to manipulative self-pollination were assessed in plants by enclosing inflorescences in loose-fitting bags constructed from cheesecloth. Self-compati-

1	1	9

Character	I. l. australis	I. l. longiflora	I. l. neomexicana
Plant height (cm)	24.1 ± 9.4 (45)	$61.0 \pm 15.6(71)$	24.9 ± 9.3 (83)
Basal stem diameter (mm)	$2.6 \pm 0.1 (45)$	$7.0 \pm 0.2 (71)$	2.8 ± 0.1 (83)
Midcauline leaf segment number	5 (3-7; 51)	7 (5-9; 71)	5 (3-7; 93)
Midcauline leaf length (mm)	$26.7 \pm 7.3 (51)$	$37.6 \pm 7.0 (71)$	$23.5 \pm 5.8 (93)$
Calyx lobe length (mm)	$3.1 \pm 0.7 (28)$	$2.1 \pm 0.3 (32)$	$3.3 \pm 0.5 (32)$
Calyx lobe apex (internal) pubescence	dense	glabrous to sparse	moderate to dense
Modal ovule number	24 (17-24; 50)	30 (22–30; 50)	30 (23-30; 50)
Capsule length (mm)	$8.8 \pm 1.1 (30)$	$11.8 \pm 1.5 (34)$	$12.5 \pm 1.7 (36)$
Capsule length/fruiting calyx length	$1.1 \pm 0.1 (30)$	$1.8 \pm 0.3 (34)$	$1.9 \pm 0.1 (36)$
Seed apex wing length (mm)	$0.1 \pm 0.0 (50)$	$0.3 \pm 0.1 (50)$	$0.6 \pm 0.2 (50)$

TABLE 2. COMPARATIVE TABLE OF DIAGNOSTIC CHARACTERS OF *IPOMOPSIS LONGIFLORA* SUBSPECIES. The mean, standard deviation, and sample size (in parentheses) are given for each quantitative character. Midcauline leaf segment number and number of ovules per ovary are reported as modes, followed by range and sample size in parentheses.

bility was assessed by emasculating flower buds prior to anthesis and anther dehiscence and directly applying pollen to stigmas using dehisced anthers from the same plant. Flowers were also permitted to complete anthesis without manipulation. Mature capsules were dissected and the number of seeds in each and counted (Table 3). The ovary of a third flower on the same plant was dissected to estimate ovule number. Chromosome counts were made by studying actively growing root tips and flower buds, using orcein in proprionic acid (modified from Smith 1974).

MORPHOLOGICAL RELATIONSHIPS, CHROMOSOME NUMBER, AND DISTRIBUTION

Several diagnostic characters separate the three subspecies (Table 2). Plants of subsp. *longiflora* are generally more than twice as tall as those of subsp. *australis* and ssp. *neomexicana*. The lower 2–10 cm of the stems are thick, sclerified, and about twice as wide at the base than in either subsp. *australis* and subsp. *neomexicana*. Cauline leaves are longer and tend to have more segments. The lowest inflorescence branches in subsp. *longiflora* usually occur above the middle, whereas in most plants of subsp. *australis* and subsp. *neomexicana* they occur well below the middle (Fig. 1). Calyx lobe length in subsp. *australis* and subsp. *neomexicana* averages about 1 mm longer than in subsp. *longiflora*. All three taxa have calvx lobes that are minutely glandular on the outer surface. However, the inner surfaces of lobe apices are moderately to densely eglandular puberulent in subsp. australis and subsp. neomexicana. Those of subsp. longiflora are either glabrous or bear only a few eglandular trichomes. Twenty-four ovules per ovary are modal in subsp. australis, as compared to 30 ovules in subsp. longiflora and subsp. neomexicana (Table 3). The fruits of subsp. neomexicana resemble those of subsp. longiflora in length and shape (Fig. 1; Table 3). Capsules are ellipsoid and about twice the length of the fruiting calyx in both taxa. Seeds of subsp. longiflora and neomexicana are narrowly ellipsoid, with a flat to slightly convex dorsal surface, and minutely winged along the margin and at the tips (Fig. 1). In subsp. australis, the capsules are ovoid to broadly ellipsoid, shorter in length, and scarcely exceed the calyx (Fig. 1; Table 2), and the seeds are essentially wingless (Fig. 1; Table 2).

The typical subspecies is a western Great Plains endemic, ranging from southwestern South Dakota (Bennett and Todd Cos.) south through western Nebraska, eastern Colorado, western Kansas, western Oklahoma, eastern New Mexico, and northwestern Texas (Fig. 2). It often occurs on sandy soils, especially sand hills in the northern plains and sandy alluvials along principal tributaries of the upper Niobrara, Platte, Republican, Arkansas, Canadian, Red, and Brazos rivers.

TABLE 3. COMPARISON OF AUTOGAMOUS VERSUS MANIPULATED SELF-POLLINATION IN *IPOMOPSIS LONGIFLORA*. Mean ovule number, mean seed number per capsule, and mean seed set, expressed as a proportion of ovule number, \pm standard error. Sample size is uniformly 50 capsules.

	I. l. australis	I. l. longiflora	I. l. neomexicana
Ovule number			
Mean ovule number	19.8 ± 0.4	27.7 ± 0.4	26.1 ± 0.5
Autogamous self-pollination			
Mean seed number	11.3 ± 0.6	10.5 ± 0.9	13.1 ± 0.8
Seed/ovule ratio	57.8 ± 3.2	38.0 ± 3.8	50.4 ± 3.1
Manipulated self-pollination			
Mean seed number	15.7 ± 0.4	18.7 ± 0.4	19.7 ± 0.5
Seed/ovule ratio	80.1 ± 1.7	67.9 ± 1.5	76.1 ± 1.5

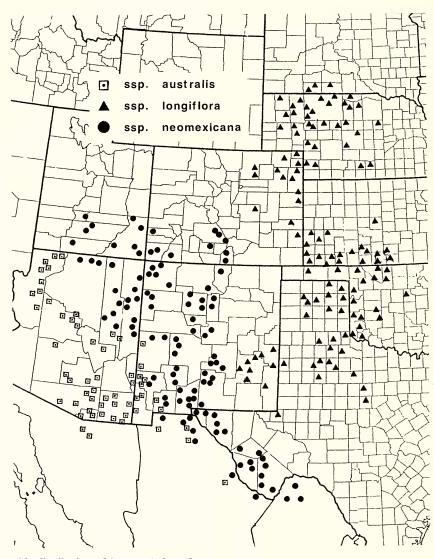


FIG. 2. Geographic distribution of *Ipomopsis longiflora*.

The distribution of subsp. australis coincides with the northeastern portion of the Sonoran Subprovince, as defined by Thorne (1993). It occurs on sandy soils of open sites in desert shrublands, grasslands, and woodlands, generally south of the Mogollon Rim in Arizona, and extending south to Sonora and northwestern Chihuahua, Mexico (Fig. 2). Subspecies neomexicana occurs in similar habitats, but its distribution coincides with the southeastern Great Basin Province and Chihuahuan Subprovince (Thorne 1993). It occurs from southeastern Utah and southwestern Colorado, through eastern Arizona and New Mexico as far south as northern Coahuila. The distribution of each subspecies is largely allopatric, although some populations of subsp. australis and subsp. neomexicana are less than 40 km apart (Fig. 2; east-central Arizona, southwestern New Mexico, and northern Chihuahua).

Grant (1959) reported 2n = 14 for plants now treated as subsp. *longiflora* (Colorado, Weld Co., Grant 9503, RSA) and subsp. *neomexicana* (New Mexico, Socorro Co., Grant 8813, RSA). Additional counts of the same number were obtained from representative populations of each subspecies (Table 1).

VEGETATIVE AND REPRODUCTIVE BIOLOGY

Field and common garden studies suggest that subsp. *longiflora* is at least a biennial, whereas subsp. *australis* and *neomexicana* are annuals. Observations of subsp. *longiflora* in the sand hills of western Nebraska (Sheridan Co.) and eastern Colorado (Logan Co.) suggest that it lives through at least two growing seasons, separated by one winter, prior to reproduction. Germination occurs during the spring (April-June) following snowmelt and late spring storms. Plants develop into vegetative rosettes that expand by additional growth during the first summer, remain dormant during the winter, followed by renewed rosette growth, shoot elongation, and reproduction during the late spring and summer months (May-September) of the second year. Plants grown to maturity from 6-month-old transplants in a common garden in Ft. Collins, Colorado required 18 months to flower. Plants grown under greenhouse conditions did not flower unless they were subjected to at least 10–12 weeks of cool, short-day conditions. In contrast, plants of subsp. australis and neomexicana, whose germination may coincide with either spring or summer monsoon precipitation, apparently complete their life cycle within 1 year. Plants of subsp. *australis* (north of Globe, Gila Co.) were recruited as seedlings during the spring and reproduced and died prior to the winter of the same year. Plants recruited during monsoon rains (July–August) over-wintered as rosettes and flowered in the succeeding spring and summer (March-September). Similar observations were made of subsp. *neomexicana* in the Rio Grande Valley of south-central Colorado (Alamosa Co.), northwestern Arizona (Apache and Coconino Cos.), and central New Mexico (Sierra Co.).

Ipomopsis longiflora is apparently pollinated by the hawkmoth, *Hyles lineata* (Grant and Grant 1965; Grant 1983). I observed unidentified hawkmoths in two populations (Table 1. subsp. *longiflora*, Logan Co., Colorado; subsp. *australis*, Gila Co., Arizona). *Hyles lineata* and *Manduca* were frequent visitors in experimental populations of all three taxa in Ft. Collins, Colorado. No other pollinator was observed on flowers of the three subspecies. Nectar is relatively high in sucrose, consistent with that expected in hawkmoth-pollinated flowers (Baker and Baker 1983; Freeman et al. 1985; Freeman and Wilken 1987).

Autogamous (unmanipulated) pollination resulted in seed/ovule ratios ranging from 38.0 in subsp. *longiflora* to 57.8 in subsp. *australis* and 50.4 in subsp. *neomexicana* (Table 3). Self-pollination of emasculated flowers resulted in seed/ovule ratios of 80.1 in subsp. *australis*, 67.9 in subsp. *longiflora*, and 76.1 in subsp. *neomexicana* (Table 3). These data provide further evidence of self-compatility reported by Grant and Grant (1965) and suggest that *l. longiflora* may experience a mixed mating system favoring selfing, resulting from self-compatibility, close proximity of style branches and upper anthers, and pollination by hawkmoths.

KEY TO *IPOMOPSIS LAXIFLORA* AND THE SUBSPECIES OF *IPOMOPSIS LONGIFLORA*

 I. Corolla tube 8–20 mm long, lobe 4–6 mm long;

 ovules 4–6 per locule
 I. laxiflora

- 1' Corolla tube 25–45 mm long, lobe 6–11 mm long; ovules 6–10 per locule *I. longiflora*
- Mature capsule ovoid to broadly ellipsoid, slightly exceeding the fruiting calyx; seed tip scarcely winged (wings < 0.1 mm long) . . . subsp. *australis*
- 2' Mature capsule ellipsoid, about twice the length of the fruiting calyx; seed tip winged (wings > 0.2 mm long)
- 3. Inflorescence branches arising above the middle of the central axis; base of stem 4–9 mm in diameter; most cauline leaves with 7 segments . . .
- 3' Inflorescence branches arising from throughout central axis; base of stem 1–4 mm in diameter; most cauline leaves with 5 segments
 - subsp. neomexicana

DISCUSSION

The three taxa comprising *Ipomopsis longiflora* share a combination of characters that are unique within the genus, including open, paniculate inflorescences, white to pale bluish, salverform corollas with tubes that exceed 20 mm in length, and pinnatifid leaves with 5-7 linear to narrowly oblong segments. Diagnostic differences among the three taxa are quantitative (Table 2), analogous to other infraspecific taxa within Ipomopsis (Grant and Wilken 1988). Ipomopsis longiflora ssp. neomexicana has no apparent autapomorphies and is separated by a combination of characters shared with either ssp. australis (e.g., habit, annual life form, inflorescence branching pattern, calyx and leaf morphology) or ssp. longiflora (ovule number, seed morphology, capsule length and shape). Its geographical distribution lies between that of the other subspecies. Other closely related taxa treated as species within Ipomopsis differ by one or more qualitative differences (e.g., leaf and inflorescence architecture, corolla morphology, anther position, filament length; see Grant 1959; Grant and Wilken 1988). Preliminary studies based on matK and ITS sequences show that the three taxa comprise a monophyletic lineage embedded within a largely unresolved polytomy of related taxa treated as species (M. Porter unpublished). Consequently, these taxa are treated as subspecies rather than as distinct species.

Like Fletcher and Wagner (1984) and Freeman et al. (1985), this study did not reveal any evidence of hybridization, parapatry (*sensu* Endler 1977), or intermediacy at the population level. Nectar-sugar composition, however, was significantly higher for sucrose in both subsp. *australis* and subsp. *neomexicana* populations near their "contact zone" in southwestern New Mexico (Freeman et al. 1985), suggesting some form of interaction. Although selection for increasing sucrose levels may be hypothesized as a consequence of gene flow, crosscompatibility among the three subspecies is unknown. Studies of the late Quaternary (Spaulding and Graumlich 1986; Van Devender et al. 1987; Wright 1976) suggest that the modern climate and vegetation of the desert Southwest and western Great Plains developed during the last 10,000– 15,000 years. Thus, the close relationships among the three subspecies and their distribution suggest a relatively recent origin and/or expansion of range, coincident with relatively rapid development of arid interior southwestern biomes.

Some populations of subsp. *australis* and subsp. *neomexicana* occur within 10–15 km of each other without apparent or significant differences in altitude, habitat, or vegetation. Notable areas of close proximity (Fig. 2) include the vicinities of Holbrook (Navajo Co., AZ) Silver City and Lordsburg (Grant Co., NM), and Samalyuca (northern Chihuahua, Mexico). Populations of subsp. *neomexicana* and subsp. *longiflora* occur within 30–40 km of each other in Chaves Co., NM. These potential contact zones may provide an opportunity to investigate the proximate causes of their respective distributions.

ACKNOWLEDGEMENTS

I thank Reggie Fletcher, Ed Freeman, Jim Henrickson, Steve O'Kane, and Warren L. Wagner for their advice, specimens, and discussions concerning this study and Bob Patterson and Mark Porter for their critical reviews. Jan Beckert skillfully composed and prepared the illustrations.

LITERATURE CITED

- CRONQUIST, A., A. HOLMGREN, N. HOLMGREN, J. REVEAL, AND P. HOLMGREN. 1984. Intermountain flora. *In* Vascular plants of the intermountain west, U.S.A., Vol. 4. New York Botanical Garden, Bronx, NY.
- ENDLER, J. 1977. Geographic variation, speciation, and clines. Princeton University Press, NJ.
- FLETCHER, R. A. AND W. L. WAGNER. 1984. A new subspecies of *Ipomopsis longiflora* (Polemoniaceae) from Arizona, New Mexico, and northern Mexico. Madroño 31:20–23.
- FREEMAN, C., W. REID, AND R. WORTHINGTON. 1985. Patterns of floral nectar-sugar composition of *Ipomopsis longiflora* (Polemoniaceae) near the contact zone of its subspecies *longiflora* and *australis*. American Journal of Botany 72:1662–1667.

- AND D. WILKEN. 1987. Variation in nectar sugar composition at the intraplant level in *Ipomopsis longiflora* (Polemoniaceae). American Journal of Botany. 74:1681–1689.
- GRANT, V. 1959. Natural history of the phlox family. Martinus Nijoff, The Hague.
- 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. Botanical Gazette 144:439–449.
- ——— AND K. GRANT. 1965. Flower pollination in the phlox family. Columbia University Press, New York.
- AND D. WILKEN. 1986. Taxonomy of the *Ipomopsis aggregata* group (Polemoniaceae). Botanical Gazette 147:359–371.
- MCKELVEY, S. 1956. Botanical exploration of the trans-Mississippi west, 1790–1850. Arnold Arboretum of Harvard University, Jamaica Plain, MA.
- SMITH, B. 1974. Cytological evidence. Pp. 237–258. In Radford, A., W. Dickison, J. Massey, and C. R. Bell, Vascular plant systematics, Harper and Row, NY.
- SPAULDING, W. AND L. GRAUMLICH. 1986. The last pluvial episodes in the deserts of southwestern North America. Nature. 320:441–444.
- THORNE, R. F. 1993. Phytogeography. Pp. 132–153. In Flora of North America Editorial Committee: Flora of North America, Vol. 1. Oxford University Press, NY and Oxford.
- VAN DEVENDER, T., R. THOMPSON, AND J. BETANCOURT. 1987. Vegetation history of the deserts of southwestern North America: The nature and timing of the late Wisconsin-Holocene transition. Pp. 323–352. In W. Ruddiman and H. Wright (eds.), The geology of North America. Geological Society of America, Boulder, Co.
- WELSH, S., N. ATWOOD, S. GOODRICH, AND L. HIGGINS. 1987. A Utah flora. Great Basin Naturalist Memoirs. 9:1–894.
- WILKEN, D. 1986. Polemoniaceae. Pp. 666–678. In The Great Plains Flora Association, Flora of the Great Plains, University Press of Kansas, Lawrence, KS.
- WRIGHT, H. 1976. The dynamic nature of Holocene vegetation, a problem in paleoclimatology, biogeography, and stratigraphic nomenclature. Quaternary Research. 6:581–596.